A REVISION OF THE CENTRAL AMERICAN SPECIES OF SMILACINA*

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I. Introduction

The genus *Smilacina* was established by Desfontaines[1] in 1807, and was based on *Convallaria racemosa* L. Linnaeus[2], in the 'Species Plantarum', first edition, had included under the generic name *Convallaria* eight species. All but one, *C. majalis*, were later segregated and referred to *Polygonatum*, *Smilacina*, and *Maianthemum*. The assemblage of these plants in one genus by Linnaeus was based principally on the spotting of the young berries, a character which is more or less common to the entire group.

Desfontaines, considering several other characters, divided *Convallaria* into four distinct genera: *Convallaria*, *Polygonatum*, *Smilacina*, and *Maianthemum*. The distinguishing features were found in the nature of the flowers and in the manner in which they are borne on the stem. *Smilacina* was distinguished because of its terminal inflorescence, the division of the perianth into six separate segments, and the star-shaped corollas.

Five species of *Smilacina* were described by Desfontaines, two of which have been collected in Mexico, namely, S. *racemosa* (*Convallaria racemosa* L.), the type species of the genus, and S. *stellata*. Of the remainder, S. *ciliata* apparently is a synonym of S. *racemosa*, S. *trifolia*, a boreal species of both hemispheres which does not enter our range, and S. *umbellata*, which becomes *Clintonia umbellulata* Michx. Bertoloni[3] added a new species in 1840, S. *flexuosa*, and was followed two years later by Martens and Galeotti[4], who described three additional species and one variety: S. *macrophylla*, S. *scilloidea*, S. *paniculata*, and S. *scilloidea* var. *acutifolia*. *Smilacina amoena* was published by Wendland[5] in 1850.

J. G. Baker[6] was the first to compose a monograph of this group, but used the earlier name *Tovaria* Necker. In this work four new species appeared: *T. thyrsoidea*, *T. laxiflora*, *T. nervulosa*, and *T. Salvini*. The first three species are regarded in this revision as synonyms of S. *paniculata* Mart. & Gal., whilst the

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[1] Desf. Ann. Mus. Par. **9**:51, *t. 9*. 1807.
[2] Linn. Sp. Pl. ed. 1. 315. 1753.
[3] Bertol. in Nov. Comm. Acad. Bonon. 4:411. *pl. 39*. 1840.
[4] Mart. & Gal. in Bull. Acad. Brux. **9**[1]:387–388. 1842.
[5] Wendl. in Otto & Dietr. Allg. Gart. Zeit. **17**:137. 1850.
[6] Baker in Jour. Linn. Soc. Bot. **14**:564. 1876.

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fourth apparently is a color variety of *S. amoena* Wendl.

In his treatment of *Smilacina* for the Botany of the 'Biologia Centrali-Americana,' Hemsley[7] merely abstracted the revision of Baker, and making the necessary transfers from *Tovaria* recognized seven species: *S. flexuosa, S. laxiflora, S. nervulosa, S. paniculata, S. Salvini, S. scilloidea,* and *S. thyrsoidea.* Like Baker, Hemsley was unable to place *S. paniculata* satisfactorily, considering it as identical with *S. amoena,* and thought *S. macrophylla* to be a synonym of *S. scilloidea.*

Since 1884 the only new species of *Smilacina* to be published from Central America and Mexico is *S. Gigas* Woodson[8], from Panama, which probably is only a giant phase of *S. paniculata* Mart. & Gal.

Because of its popularity and general use, the generic name *Smilacina* was conserved by the International Botanical Congress of Brussels (1910), since it is antedated by three previous genera: *Vagnera* Adans.[9], *Tovaria* Neck.[10], and *Polygonastrum* Moench[11]. Later generic synonyms include *Sigillaria* Raf.[12], *Stylandra* Raf.[13], *Asteranthemum* Kunth[14], *Jocaste* Kunth[15], *Medora* Kunth[16], and *Neolexis* Salisb.[17], all of which fall readily into synonymy.

II. Morphology and Generic Relationships

Roots.—The roots of *Smilacina* are borne either at the nodes or all over the surface of the underground rhizome. They are either simple or shortly branched, closely placed to one another and forming a dense mass as in *S. amoena* var. *Salvini,* or more loosely clustered at the nodes as in *S. scilloidea.* They are relatively slender and sometimes very long, measuring a foot or more in length. They are usually covered with a dense felt of persistent root hairs.

Rhizome.—The rhizome varies considerably both in size and in some external characters such as type of branching. But due to the difficulty in pressing these large underground stems, they are seldom collected and not much is known of their variability or taxonomic importance. They are essentially simple or branched, and apparently reach relatively great lengths in most species. They may be thick and very fleshy as in *S. amoena* var. *Salvini,* or quite slender as in *S. scilloidea.* The rhizome of *S. racemosa* is very knotty due to the closely budding upright shoots, while those of *S. scilloidea* and *S. stellata* are rather smooth and slender, since there is less budding.

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[7] Hemsl. Biol. Centr.-Am. Bot. **3**:367–368. 1884.
[8] Woodson in Ann. Mo. Bot. Gard. **27**:270. 1940.
[9] Adans. Fam. Pl. **2**:496. 1763.
[10] Neck. Elem. **2**:190. 1790.
[11] Moench, Meth. 637. 1794.
[12] Raf. in Jour. Phys. **89**:261. 1819.
[13] Raf., loc. cit. 102. 1819.
[14] Kunth, Enum. Pl. **5**:151. 1850.
[15] Kunth, loc. cit. 154. 1850.
[16] Kunth, loc. cit. 155. 1850.
[17] Salisb. Gen. Pl. Fragm. 64. 1866.

Stems.—The stems are erect, unbranched, and typically herbaceous, arising from the terminal bud of the rhizome. The basal portion usually is clothed with very thin, scale-like, sheath leaves from the terminal bud of the rhizome. The height of the stem varies from 0.2 to 3 m., and may be relatively constant as in S. *amoena*, S. *racemosa* and most of the other species, or extremely variable, as in S. *paniculata*. In the living state the color varies from green to somewhat reddish or purplish at the base or in the inflorescence.

Leaves.—The leaves are alternate, and may be either sessile or petiolate. They vary in shape from narrowly lanceolate to broadly elliptic. In length they measure from about 3 to 30 cm. with the same extremes in width. All have longitudinal primary veins, some of which branch from near the leaf-base and are more prominent than the others. The number of these principal veins is rather constant for certain species, but is often difficult to observe. The great majority of the species bear glabrous leaves, but in some plants of S. *flexuosa*, and generally in S. *stellata*, there is an inconspicuous pubescence. The leaf characters vary considerably in the genus, and often even in the same species. It would be difficult to delimit the species by using such characters because of their inconsistency amongst individuals clearly conspecific in other details.

Inflorescence.—The inflorescence of *Smilacina* is terminal, or very rarely with auxilliary inflorescences in the axils of the uppermost leaves. Bracts usually are apparent only at the lower nodes. The best characters for the distinction of the species are found in the form of the inflorescence. These characters are shown in the diagrams of fig. 1, which also is a good indication of the probable phylogeny within the genus. There apparently is an evolutionary series from a diffuse panicle to a typical raceme, resulting through the suppression of secondary peduncles.

In S. *paniculata* and S. *racemosa* the inflorescence is a typical panicle, the secondary peduncles being extensive and many-flowered. The pedicels are relatively short, scarcely longer than the perianth and occasionally even somewhat shorter. In S. *amoena* the paniculate structure is less obvious, and the secondary peduncles have become shortened and few-flowered; and the pedicels are much longer than the perianth.

The secondary peduncles have become completely reduced, or rarely only slightly manifest in S. *flexuosa*, S. *scilloidea*, and S. *macrophylla*. The chief indication of a previous compound nature is found in the clustering of the flowers at the nodes of the primary peduncle. In S. *flexuosa* the rachis is conspicuously flexuous or geniculate, and the flowers are borne in groups of twos, threes, or occasionally fours. In this species the pedicels elongate very conspicuously after anthesis. The rachis is essentially straight in S. *scilloidea*, and is scarcely stouter than the pedicels, which occur usually in twos. In S. *macrophylla* the inflorescence

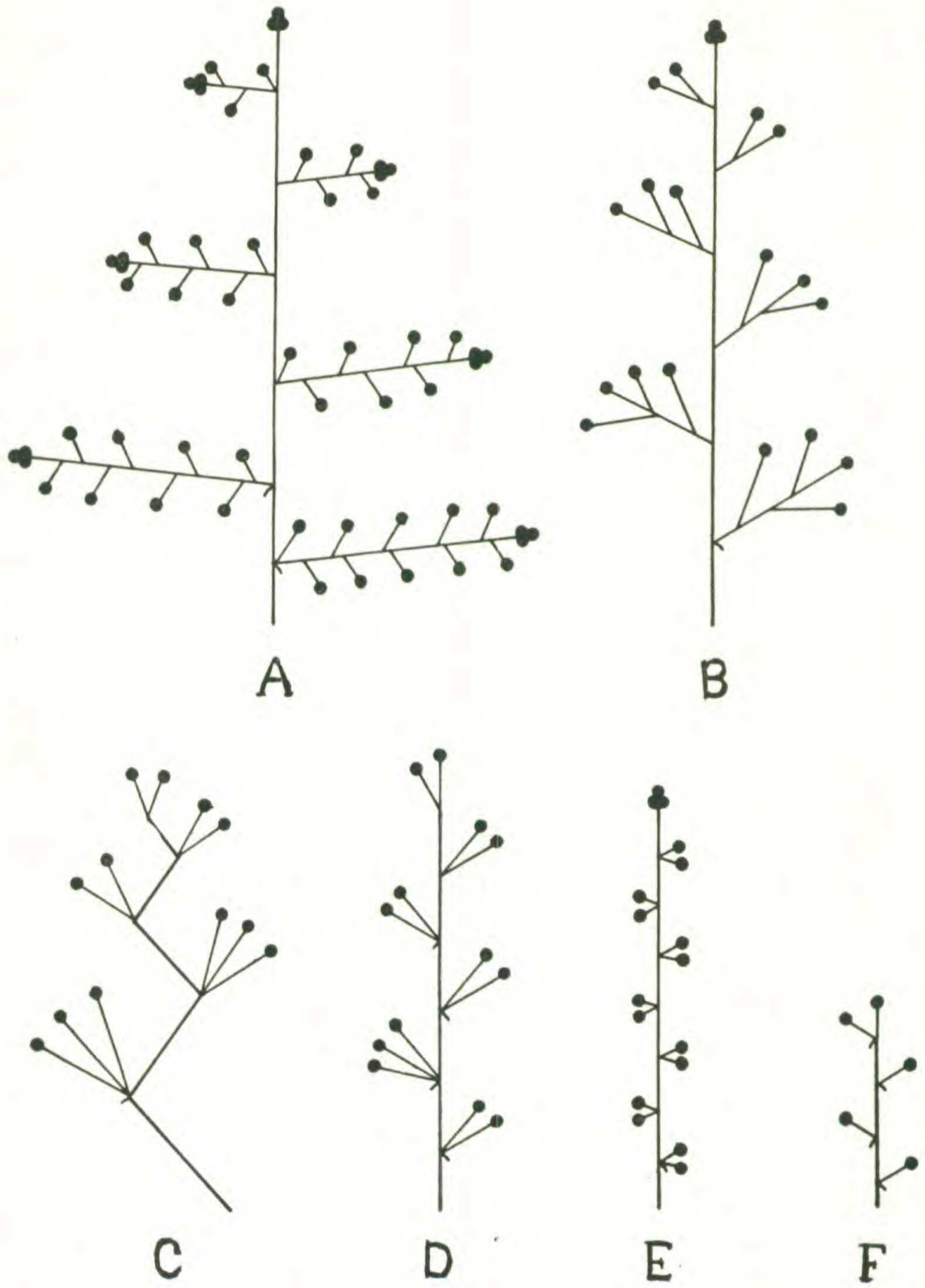

Figure 1. Inflorescence structures in *Smilacina:* A, *S. paniculata;* B, *S. amoena,* C, *S. flexuosa;* D, *S. scilloidea;* E, *S. macrophylla,* F, *S. stellata.*

is subspiciform, with a straight, stout rachis bearing short, horizontal or reflexed, paired pedicels.

The reduction of the inflorescence to a typical raceme is attained in *S. stellata,* where the pedicels are borne singly at the nodes.

Perianth.—In *Smilacina,* as in most Liliaceae, there is no distinction of calyx

and corolla except in the separation of the six segments into an outer and an alternating inner whorl. The outer and inner segments are exactly alike in shape and size, varying amongst the different species from lanceolate to broadly ovate in outline, and in length from 1 mm. *(S. racemosa)* to 9 mm. *(S. flexuosa)*. They may be widely spreading at anthesis, as in S. *paniculata*, or nearly erect and overlapping, as in S. *amoena* and S. *macrophylla*. The former condition is by far the more common. The perianth of *Smilacina* predominantly is white, but three closely related species, S. *flexuosa*, S. *scilloidea*, and S. *amoena*, include varieties with pink or flesh-colored flowers *(S. flexuosa* var. *rosea*, S. *scilloidea* var. *erubescens*, and S. *amoena* var. *Salvini)*. This parallelism in color variation is very suggestive of close relationship amongst the three species.

Stamens.—There are six stamens in flowers of *Smilacina*, and these are attached to the base of the perianth segments. The anthers are introrse, 4-celled, and split longitudinally at anthesis. They vary from 0.5 to 3.0 mm. in length, and are commonly yellowish, but sometimes blue, at least in S. *paniculata*. The filaments may be narrowly filiform or somewhat enlarged at the base, varying from about 1 mm. in length in S. *racemosa* to 4 mm. in S. *flexuosa*.

Pistil.—The pistil is typically liliaceous, being 3-carpellate and 3-celled. The style may be somewhat shorter or somewhat longer than the ovary, and is capped by the stigma which is more or less deeply 3-lobed. *Smilacina* previously has been described as having two ovules within each loculus of the ovary, but during this investigation it has been found that the number varies from 1, in some flowers of S. *flexuosa* and S. *paniculata*, to 5 or 6 in S. *amoena*. Although the number of ovules is not a constant character for the species, there is a general tendency toward a constant number in each species.

Fruit.—The fruit is a one- to several-seeded berry, more or less deeply 3-lobed. It is some shade of red or dark purple at maturity, rather spotted when young.

The closest relatives of *Smilacina* in North America are the genera *Convallaria* L., *Maianthemum* Desf., *Clintonia* Raf., and *Polygonatum* Desf. These may be distinguished as follows:

a. Perianth segments free.
  b. Stems leafy; leaves cauline, alternate; inflorescence paniculate to racemose.
    c. Flowers hexamerous ..... SMILACINA Desf.
    cc. Flowers tetramerous ..... MAIANTHEMUM Desf.
  bb. Stems scapiform; leaves basal; inflorescence umbellate ..... CLINTONIA Raf.
aa. Perianth segments coherent.
  b. Stems leafy; cauline leaves alternate; inflorescence axillary ..... POLYGONATUM Desf.
  bb. Stems scapiform; leaves basal; inflorescence terminal ..... CONVALLARIA L.

III. GEOGRAPHIC DISTRIBUTION

Smilacina is an outstanding example of the numerous genera having a common distribution in eastern Asia and eastern North America, to which Asa Gray called attention many years ago. In Asia the genus extends from Siberia to Japan and the Himalaya Mountains, represented by perhaps a dozen species. In North America its distribution ranges from Newfoundland to Alaska, southward to Panama.

In Mexico and Central America the genus is found only in the mountains at elevations of 1300–3300 m., usually in association with *Quercus*, *Alnus*, and other northern plant types. In such associations the plants of *Smilacina* frequently are common and terrestrial, but also grow on old stumps and mossy tree trunks from seeds probably deposited by birds after eating the pulpy berries.

Smilacina racemosa and S. *stellata*, which occur widely in the United States and northward, are found in Mexico only in the Sierra Madre of Chihuahua. But the majority of species have their center of distribution in Guatemala, extending northward to the Mexican States of Vera Cruz and Puebla and southward to the Province of Chiriquí, Panama. This distribution is that of S. *paniculata*, which is the most widespread of those in Mexico and Central America, as well as probably the most primitive of the species under discussion.

Smilacina amoena and S. *flexuosa* are nearly as widely distributed as S. *paniculata*, and occur throughout about the same territory from southeastern Mexico to Costa Rica. *Smilacina scilloidea* has been collected in Mexico, Honduras, and Guatemala, whilst S. *macrophylla* apparently is confined to southern Mexico. *Smilacina* apparently has not yet been found in Nicaragua, and only one doubtful specimen has been collected in Honduras. Future collections in those countries will surely show it to occur in the higher mountains, and help to explain some of the unsolved problems of this investigation.

IV. TAXONOMY

Smilacina Desf. in Ann. Mus. Paris **9**:51, *t. 9*. 1807; Endl. Gen. 1183. 1836-40; Benth. & Hook. Gen. Pl. **3**:770. 1883; Hemsl. Biol. Centr.-Am. Bot. **3**:367. 1884; Engl. in Engl. & Prantl, Nat. Pflanzenfam. ed. 1. **2**^{4}:79. 1888, *nomen conservandum.*

Vagnera Adans. Fam. Pl. **2**:496. 1763, *nomen rejiciendum.*
Tovaria Neck. Elem. **2**:190. 1790; J. G. Baker in Jour. Linn. Soc. Bot. **14**:564. 1876; Krause in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. **15**^{a}:367. 1930, *nomen rejiciendum.*
Polygonastrum Moench, Meth. 637. 1794, *nomen rejiciendum.*
Sigillaria Raf. in Jour. Phys. **89**:261. 1819.
Stylandra Raf. loc. cit. 102. 1819.
Asteranthemum Kunth, Enum. Pl. **5**:151. 1850.
Jocaste Kunth, loc. cit. 154. 1850.
Medora Kunth, loc. cit. 155. 1850.
Neolexis Salisb. Gen. Pl. Fragm. 64. 1866.

Perianth homochlamydeous, equally 6-parted, white to pink or purplish. Stamens 6, epipetalous, the filaments filiform or dilated, the anthers introrse, 4-celled. Ovary superior, 3-carpellate, the loculi with 1–6 superposed anatropous ovules on an axile placenta, the style terminal, filiform, the stigma capitate or somewhat 3-lobed. Berries pulpy, usually red or purplish, 1–6-seeded. Herbs with simple stems from an extensive rhizome. Leaves alternate, shortly petiolate to sessile or somewhat amplexicaul, with 3 to many principal parallel veins and variable secondary and cross veins. Inflorescence usually terminal, occasionally in the upper leaf axils also, paniculate to racemose, bracts very small or lacking.

Type species: *Smilacina racemosa* (L.) Desf.

Specimens have been examined from five of the larger herbaria of the United States. These are abbreviated in the citation of exsiccatae as follows: Chicago Museum of Natural History (formerly Field Museum) (FM); Gray Herbarium of Harvard University, Cambridge, Mass. (GH); Missouri Botanical Garden, St. Louis (MBG); University of California, Berkeley (UC); United States National Herbarium, Washington (US). I am very grateful to the curators of these herbaria for their courtesy and interest, and particularly to Dr. J. M. Greenman, Curator of the Missouri Botanical Garden Herbarium, under whom this investigation was carried on.

KEY TO THE SPECIES AND VARIETIES

a. Inflorescence paniculate, the lateral branches of the rachis manifest (but the upper ones much reduced in S. *amoena*).
  b. Inflorescence typically paniculate, the lateral branches of the rachis many-flowered; pedicels scarcely longer than the perianth.
    c. Perianth segments 3–5 mm. long; anthers included ..... *1. S. paniculata*
    cc. Perianth segments 1.0–1.5 mm. long; anthers exserted ..... *2. S. racemosa*
  bb. Inflorescence subracemiform, the lateral branches of the rachis corymbose, less manifest and few-flowered, the upper ones much reduced; pedicels much longer than the perianth.
    c. Flowers white ..... *3. S. amoena*
    cc. Flowers pink ..... *3a. S. amoena* var. *Salvini*

aa. Inflorescence subracemose, the lateral branches of the rachis not manifest, or only rarely so, the flowers paired or clustered at the nodes.
  b. Inflorescence racemiform, the rachis scarcely stouter than the pedicels, the latter usually horizontal or ascending; perianth segments spreading, oblong-lanceolate, 2–3 times as long as broad.
    c. Rachis flexuous or geniculate; pedicels longer than the perianth; principal veins of leaves usually 5–7.
      d. Flowers white ..... *4. S. flexuosa*
      dd. Flowers purplish pink ..... *4a. S. flexuosa* var. *erubescens*
    cc. Rachis straight; pedicels as long as the perianth or somewhat shorter; principal veins of leaves usually 3.
      d. Flowers white ..... *5. S. scilloidea*
      dd. Flowers pink ..... *5a. S. scilloidea* var. *rosea*
  bb. Inflorescence subspiciform, the rachis straight, much stouter than the pedicels, the latter descending; perianth segments nearly erect, broadly oval, almost as broad as long ..... *6. S. macrophylla*

aaa. Inflorescence typically racemose, the rachis unbranched, the flowers solitary in the axils of minute bracts ..... *7. S. stellata*

1. Smilacina paniculata Mart. & Gal. in Bull. Acad. Brux. 9²:388. 1842.

Tovaria thyrsoidea J. G. Baker in Jour. Linn. Soc. Bot. 14:568. 1876.
Tovaria laxiflora Baker, loc. cit. 569. 1876.
Tovaria nervulosa Baker, loc. cit. 1876.
Smilacina thyrsoidea (Baker) Hemsl. Biol. Centr.-Am. Bot. 3:368. 1884.
Smilacina laxiflora (Baker) Hemsl. loc. cit. 1884.
Smilacina nervulosa (Baker) Hemsl. loc. cit. 1884
Smilacina Gigas Woodson, Ann. Mo. Bot. Gard. 27:270. 1940.

Stems 0.4–3 m. high, somewhat flexuous, glabrous; leaves shortly petiolate, narrowly lanceolate to broadly ovate, acuminate, 6–30 cm. long, 1–12 cm. broad, longitudinal veins closely parallel and equal, or widely separated with 3–8 prominent veins and less conspicuous intermediate parallel veins, lateral veins more or less visible in dried plants; inflorescence typically paniculate, the secondary branches extensive and many-flowered, 3–50 cm. long, 2–25 cm. broad; pedicels solitary, horizontal or ascending, 1–10 mm. long; flowers white; perianth segments ovate-lanceolate, 3–5 mm. long, 1.5–2.5 mm. broad, spreading; stamens included, 2–4 mm. long, filaments somewhat enlarged at base, 1–3 mm. long, anthers 0.5–2.5 mm. long; ovary and style about equal in length, 1–5 ovules in each loculus, 1–2 ovules most common; fruit 1–5-seeded.

MEXICO: VERA CRUZ: Orizaba, *Botteri 138* (GH, US); in wet forest, in region of Orizaba, *Botteri 914* (US); in moist mountain forest, Cerro de Chocoman, Canton Córdoba, May 12, 1907, *Seler & Seler 5174* (US, GH); Acultzinco, May 1, 1937, *Matuda 1161* (US). PUEBLA: ledges of barranco below Honey Station, alt. 1525 m., May 6, 1904, *Pringle 8836* (UC, FM, GH, MBG, US). OAXACA: Teotalcingo, Petlapa, alt. 800–1400 m., *Galeotti 5485* (GH, UC, US); Petlapa, June, *Liebmann 14637* (FM). CHIAPAS: Cerro del Boquerón, Aug. 1913, *Purpus 7022* (UC).

GUATEMALA: ALTA VERAPAZ: on stumps and banks, Chama to Cobán, alt. 1075 m., Aug. 23, 1920, *Johnson 639* (US); forest near Cobán, alt. 1600 m., Sept. 1907, *Tuerckheim II 1962* (GH, US); Pansamalá, alt. 1125 m., May 1887, *Tuerckheim 231* (US). SAN MARCOS: hanging from tree at upper edge of potrero, Volcán Tajumulco, alt. 1300–1350 m., March 13, 1940, *Steyermark 37655* (FM). BAJA VERAPAZ: damp forest, mountain side north of divide north of Santa Rosa, alt. 1650 m., March 30, 1939, *Standley* 69927 (FM).

COSTA RICA: CARTAGO: Volcán Irazú, alt. 3050–3450 m., Dec. 1, 1937–Jan. 1, 1938, *Allen 690* (FM); in the oak forest on the upper slopes, El Volcán Irazú, Aug. 18, 1925, *Dodge 3417* (GH, US); south slope of Volcán Irazú near Finca Chilena, alt. 2700–2900 m., March 4, 1930, *Dodge & Thomas 8073* (GH, MBG); southern slope of western or main cone of Irazú, above alt. 3050 m., July 31, 1937, *Hatch 178* (FM); vicinity of the crater of the Volcán Irazú, Aug. 24, 1935, *Quiros 336* (FM); southern slope of Volcán de Irazú, March, 1924, *Standley 36629* (US); southern slope of Volcán de Turrialba, near the Finca del Volcán de Turrialba, alt. 2000–2400 m., Feb. 22, 1924, *Standley 35186* (US). SAN JOSÉ: on tree in wet forest, near Finca la Cima, above Los Lotes, north of El Copey, alt. 2100–2400 m., Dec. 21–22, 1925, *Standley 42735* (US); La Hondura, alt. 1300 m., Aug. 15, 1933, *Valerio 790* (FM).

PANAMA: CHIRIQUÍ: vicinity of "New Switzerland", central valley of Río Chiriquí Viejo, alt. 1800–2000 m., Jan. 6–14, 1939, *Allen 1392* (MBG); trail from Cerro Punta to headwaters of Río Caldera, alt. 2250–2500 m., Jan. 14, 1939, *Allen 1446* (MBG); rain forest, Bajo Chorro, alt. 1825 m., Jan. 6, 1938, *Davidson 53* (FM); Volcán de Chiriquí, Boquete District, alt. 2900 m., July 16, 1938, *Davidson 990* (FM); Volcán de Chiriquí, alt. 3300 m., Feb. 27, 1918, *Killip 360* (US); forest edge, vicinity El Potrero Camp, Chiriquí Volcano, alt. 2800–3000 m., March 10–13, 1911, *Pittier 3071* (US); on rotten stumps, Valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–

1900 m., June 27–July 13, 1935, *Seibert 184* (GH, MBG); vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 852* (MBG); Loma Larga to summit, Volcán de Chiriquí, alt. 2500–3380 m., July 4–6, 1938, *Woodson, Allen & Seibert 1034* (MBG); valley of the upper Río Chiriquí Viejo, March 18, 1938, *P. White 57a* (MBG); valley of the upper Río Chiriquí Viejo, Summer 1937, *P. White 75* (MBG); vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., July 18, 1940, *Woodson & Schery 512* (MBG); Casita Alta to Cerro Copete, alt. 2300–3300 m., July 10, 1940, *Woodson & Schery 339, 341, 342* (MBG).

This species is extremely variable in size, ranging from 0.4 to 3.0 m. tall. The leaves are proportionately variable also. The inflorescence may be small, measuring only 3 cm. long and 2 cm. broad, or it may be large and spreading, 50 cm. long and 25 cm. broad.

2. Smilacina racemosa (L.) Desf. in Ann. Mus. Par. **9**:51. 1807.

Convallaria racemosa L. Sp. Pl. 315. 1753.
Tovaria racemosa Neck. Elem. **3**:190. 1790.
Polygonastrum racemosum Moench, Meth. 637. 1794.
Maianthemum racemosum Link, Enum. **1**:343. 1821.
Unifolium racemosum Britton in Trans. N. Y. Acad. Sci. **8**:74. 1889.
Vagnera racemosa Morong in Bull. Torr. Bot. Club **20**:480. 1893.

Stems 1.8–7.8 dm. high, flexuous, glabrous or slightly pubescent; leaves sessile or shortly petiolate, lanceolate-ovate, acuminate, under leaf-surface inconspicuously pubescent, chiefly lower portion and petiole, 3–4 times as long as broad, 6–15 cm. long, 1.5–5.5 cm. broad, many major and minor longitudinally parallel veins, lateral veins hidden; inflorescence typically paniculate, lateral branches several-flowered, 2.5–10.5 cm. long, 0.5–2.5 cm. broad; pedicels solitary, usually ascending or horizontal, 0.5–2 mm. long; flowers white; perianth segments lanceolate or oblong, 1.0–1.5 mm. long, 0.5 mm. broad; stamens exserted, 2–3 mm. long, filaments enlarged at the base, 1.5–2.5 mm. long, anthers 0.5 mm. long; style shorter than the ovary, 2 ovules in each loculus; fruit 1–several-seeded.

MEXICO: CHIHUAHUA: near Colonia Garcia in the Sierra Madres, alt. 2285 m., June 3, 1899, *Townsend & Barber 5* (FM, MBG, US); Las Cuevas, June 30, 1892, *Hartmann 544* (GH, US) cold ledges, Sierra Madre, Oct. 3, 1887, *Pringle 1487* (GH); Sierra Madre, 1899, *Townsend & Barber 8* (US).

With so few specimens, it appears unprofitable to attempt the association of our Central American *S. racemosa* with either var. *typica* or var. *cylindrata* as segregated by Fernald (in Rhodora **40**:406-407. 1938). Amongst even our four specimens, extent of branching and general shape of the inflorescence are quite variable, suggesting the hopeless variability in *S. paniculata*. Evaluation of the reported geographical gradient in *S. racemosa* of the United States is without the scope of this discussion.

3. Smilacina amoena Wendl. in Otto & Dietr. Allg. Gart. Zeit. **17**:137. 1850.

Tovaria paniculata Baker, loc. cit. 568. 1876, as to description and specimens cited, not *Smilacina paniculata* Mart. & Gal.
Smilacina paniculata Mart. & Gal. acc. to Hemsl. Biol. Centr.-Am. Bot. **3**:368. 1884, excluding specimens cited.

Stems 1.5–8.0 dm. high, somewhat flexuous, glabrous; leaves sessile and amplexicaul or shortly petiolate, narrowly ovate to broadly ovate-acuminate, 5–20 cm. long, 2–8 cm. broad, glabrous, 4–12 prominent longitudinal veins, with numerous and less conspicuous parallel veins between, lateral veins visible in dried plants; inflorescence subracemiform, not flexuous, 5–30 cm. long, 1.5–10 cm. broad; secondary branches much reduced above, few-flowered; pedicels 4–30 mm. long, horizontal or ascending; flowers white; perianth segments narrowly elliptic-obovate, 5–6 mm. long, 2.5–3.0 mm. broad, somewhat spreading; stamens included, 4 mm. long, filaments less than 1 mm. broad at the base, 3 mm. long, anthers 1.0–1.5 mm. long; ovary and style about equal in length, 4–6 ovules in each loculus; mature fruit little known.

MEXICO: VERA CRUZ: Nogales, May 2, 1937, *Matuda 1154* (MBG, US). CHIAPAS: 1864–1870, *Ghiesbreght 708* (GH, MBG).

GUATEMALA: ZÁCAPA: cloud forest in ravine bordering Quebrada Alejandria, summit of Sierra de las Minas, vicinity of Finca Alejandria, alt. 2500 m., Oct. 13, 1939, *Steyermark 29875* (FM). CHIMALTENANGO: Calderas, Oct. 25, 1937, *Johnson 1109* (FM).

COSTA RICA: SAN JOSÉ: on tree in wet forest, near Finca la Cima, above Los Lotes, north of El Copey, alt. 2100–2400 m., Dec. 21–22, 1925, *Standley 43587* (US); high plateau, alt. 2000 m., Jan. 23, 1935, *Valerio 1075* (FM). ALAJUELA: San Ramón, April 21, 1929, *Brenes 6828* (FM).

3a. **Smilacina amoena** var. **Salvini** (Baker) Emons, n. comb.

Tovaria Salvini J. G. Baker in Jour. Linn. Soc. Bot. **14**:567. 1876.
Smilacina Salvini (Baker) Hemsl. Biol. Centr.-Am. Bot. **3**:368. 1884.

Essentially the same as *S. amoena* but with flowers pink; perianth segments broadly elliptic, 6 mm. long, 3.5–4.5 mm. broad, erect.

GUATEMALA: CHIMALTENANGO: Bosques de la Sierra "Santa Elena", Tecpam, alt. 2500 m., Jan. 1, 1932, *Salas 1430* (FM); Tecpam, alt. 2740 m., Feb. 5, 1937, *Johnson 633* (FM); Santa Elena, 1933, *Skutch 232* (US); place not recorded, Jan. 1892, *Shannon 439* (US); Chicoy, alt. 2500 m., March 1892, *Shannon 358* (US); Volcán Zunil, alt. 2500–3800 m., Jan. 22, 1940, *Steyermark 34685* (FM); above Tecpam, March 11, 1931, *Collins & Kempton 21* (US); Cupressus forest, Cerro de Tecpam, region of Santa Elena, alt. 2400–2700 m., Dec. 26, 1938, *Standley 61123* (FM). QUEZALTENANGO: Volcano of Santa María, alt. 2400–3510 m., Jan. 24, 1896, *Nelson 3700* (GH, US). SAN MARCOS: along Quebrada Canjula, between Sabinal and Canjula, Volcán Tacana, alt. 2200–2500 m., Feb. 18, 1940, *Steyermark 36024* (FM); between San Sebastián and top of ridge of Volcán Tajumulco, alt. 3800–4000 m., Feb. 16, 1940, *Steyermark 35903* (FM). HUEHUETENANGO: on mountain between Sija and Huehuetenango, alt. 3000 m., Feb. 21, 1938, *Walsh s. n.* (MBG).

4. **Smilacina flexuosa** Bertol. in Nov. Comm. Acad. Bonon. **4**:411. *pl. 39.* 1840; Hemsl. Biol. Centr.-Am. Bot. **3**:367. 1884.

Smilacina Bertolonii Kunth, Enum. **5**:151. 1850.
Tovaria flexuosa (Bertol.) Baker in Jour. Linn. Soc. Bot. **14**:567. 1876.
Convallaria flexuosa Druce, Rept. Bot. Exch. Club Brit. Isl. **3**:408. 1914.
Vagnera flexuosa Standl. in Jour. Wash. Acad. Sci. **15**:457. 1925.

Stems 0.3–9 dm. high, more or less straight, glabrous or pubescent; leaves subsessile to shortly petiolate, narrowly lanceolate to broadly ovate and shortly acuminate, 6–22 cm. long, 1.2–7 cm. broad, 5–7 prominent longitudinal veins,

intermediate ones less conspicuous, numerous short lateral veins; inflorescence racemiform, 5–30 cm. long, 2–6 cm. broad; rachis geniculate or flexuous; pedicels paired or clustered at the nodes, 0.7–3 cm. long, scarcely thinner than the rachis, horizontal or ascending; flowers white; perianth segments oblong-lanceolate, 5–9 mm. long, 2–2.5 mm. broad, spreading; stamens included, 3–4 mm. long, filaments slightly enlarged at the base, 2–3 mm. long, anthers about 1 mm. long; style somewhat longer than the ovary, stigma slightly lobed, 1–2 ovules in each loculus, usually 1; fruit usually 1–4-seeded.

MEXICO: CHIAPAS: Cerro del Boquerón, Aug., 1913, *Purpus 7022* (US); damp forests, mountains east of Fenix or Phoenix, date lacking, *Purpus 10621* (US); Cerro del Boquerón, June, 1914, *Purpus 7416* (FM, UC, US); Chicharras, alt. 3000–6000 ft., Feb. 6, 1896, *Nelson 3762* (US).

GUATEMALA: ALTA VERAPAZ: near Tactic, alt. about 1500 m., April 5, 1939, *Standley 70485* (FM); San Martín, July 1, 1938, *Johnston 1305* (FM). BAJA VERAPAZ: Taltic, alt. 1400 m., April, 1882, *Lehmann 1315* (US). HUEHUETENANGO: Concepción bei San Martín im Gebüsch, alt. 2000 m., June 21, 1896, *Seler & Seler 3168* (GH, US). SAN MARCOS: shaded moist ravine slopes, between San Rafael and Guatemala-Mexico line, alt. 2500–3000 m., Feb. 21, 1940, *Steyermark 36321* (FM); barrancos 6 miles south and west of town of Tajumulco, alt. 2300–2800 m., Feb. 26, 1940, *Steyermark 36618* (FM); along road above Barranco Eminencia, alt. about 2700 m., March 14, 1939, *Standley 68568* (FM). JALAPA: Volcán Jumay, north of Jalapa, alt. 1300–2200 m., Dec. 1, 1939, *Steyermark 32400* (FM). CHIMALTENANGO: Chichavac, alt. 2400–2700 m., Nov.-Dec., 1930, *Skutch 73* (US); Cerro de Tecpam, region of Santa Elena, alt. about 2700 m., Dec. 4, 1938, *Standley 58708* (FM); region of Las Calderas, alt. 1800–2100 m., Nov. 22, 1938, *Standley 57810* (FM). SACATEPEQUEZ: slopes of Volcán de Agua, above Santa María de Jesús, alt. 2250–3000 m., Feb. 11, 1939, *Standley 65134* (FM); Volcán Agua, alt. 9500 ft., Feb. 8, 1908, *Kellerman 7295* (FM). SANTA ROSA: Santa Rosa, alt. 840 m., June, 1892, *Heyde & Lux 3527* (US); Volcán de Agua, alt. 2800 m., June, 1892, *Shannon 3634* (US).

EL SALVADOR: Cerro de Apaneca, 1928, *Calderon 2417* (FM).

HONDURAS: in forest near summit of the range above El Achote, in cloud zone above the plains of Siguatepeque, alt. 1850 m., Aug. 1, 1936, *Yuncker, Dawson & Youse 6267* (FM).

COSTA RICA: CARTAGO: El Muneco, alt. 5000 ft., June 19, 1928, *Stork 2714* (FM).

4a. **Smilacina flexuosa** Bertol. var. **erubescens** Emons, n. var.[18]

Flowers pink; otherwise essentially the same as the species.

MEXICO: CHIAPAS: Cerro del Boquerón, June, 1914, *Purpus 7415* (FM, GH, UC); Volcán Tacana, Chiquihuite, March 27, 1939, *Matuda 2846* (FM).

GUATEMALA: GUATEMALA: locality lacking, 1939, *Aguilar 232* (FM). ZACÁTEPEQUEZ: Volcán de Agua, alt. 2800 m., *J. D. Smith 2175* (US). QUICHE: Nebaj, alt. 1930 m., April, 1890, *Heyde & Lux 4647* (GH, US). SANTA ROSA: Zamorora, alt. 1535 m., April, 1893, *Heyde & Lux 4652* (GH, US). SAN MARCOS: between Todos Santos and Finca El Porvenir, alt. 1300–3000 m., March 1, 1940, *Steyermark 36972* (FM, TYPE); San Martín, Oct. 9, 1938, *Johnston 1305* (FM).

5. **Smilacina scilloidea** Mart. & Gal. in Bull. Acad. Brux. 9[2]:388. 1842.

Smilacina scilloidea var. *acutifolia* Mart. & Gal. loc. cit. 1842.
Tovaria scilloidea [*scilloides*] (Mart. & Gal.) Baker in Jour. Linn. Soc. Bot. 14:567. 1875 (?), misspelling.

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[18] **Smilacina flexuosa** Bertol. var. **erubescens** Emons, var. nov., ab specie floribus roseis praecipue differt.

Stems 1.5–8 cm. high, flexuous, glabrous; leaves slightly sessile to petiolate, narrowly lanceolate to ovate, shortly acuminate, 3.5–10 cm. long, 1.0–4.5 cm. broad, usually with about 3 major longitudinal veins and numerous minor ones between, lateral veins evident in dried plants; inflorescence racemiform, 4–6 cm. long, 1.3–2.5 cm. broad; rachis straight, pedicels usually paired at the nodes, 3–6 mm. long, scarcely thinner than the rachis, horizontal or ascending; flowers white; perianth-segments oblong-lanceolate, usually 4–5 mm. long, rarely 6 mm., 1–2 mm. broad, spreading; stamens included, about 3 mm. long, filaments 1.5–2 mm. long, anthers 1 mm. or less long; style and ovary usually about equal length, style sometimes longer, stigma slightly 3-lobed, 1–2 ovules in each loculus, commonly 2; mature fruit several-seeded.

MEXICO: MICHOACÁN: vicinity of Morelia, Cerro Azul, alt. 2200 m., 1910, *Arsène 5766* (MBG, GH); vicinity of Morelia, Companario, alt. 2100 m., Dec. 1910, *Arsène 5803* (US). OAXACA: 2230–2500 m., *Galeotti 5483* (US); Cerro San Felipe, alt. 3000 m., May 22, 1898, *Conzatti & Gonzalez 704* (GH, US); rich canyons, Sierra de San Felipe, alt. 2230–2740 m., May 22, 1894, *Pringle 4647* (GH, MBG, UC, US); northwest slope of Mt. Zempoaltepec, alt. 2230–3045 m., July 10, 1894, *Nelson 667* (US); San Miguel, alt. 3000 m., May 1917, *Reko 3840* (US); Lachopa, June 1841, *Liebmann 14630* (FM). CHIAPAS: 1864-1870, *Ghiesbreght 707* (GH, MBG); Cerro del Boquerón, June 1914, *Purpus 7416* (GH, MBG); District of Temascaltepec, Nanchititla, Aug. 12, 1933, *Hinton 4520* (FM, MBG, US); Cajones, July 9, 1935, *Hinton 7953* (MBG, US); oak woods, Temascaltepec, Nov. 8, 1933, *Hinton 5078* (FM).

HONDURAS: COMAYAGUA: in the forest near the summit of the range above El Achote, in cloud zone above the plains of Siguatepeque, alt. 1850 m., Aug. 1, 1936, *Yuncker, Dawson & Youse 6257* (FM, MBG).

5a. Smilacina scilloidea Mart. & Gal. var. **rosea** Emons, n. var.[19]

Flowers pink; otherwise essentially the same as the species.

GUATEMALA: CHIMALTENANGO: in open pine forest with dense tussock grass, slopes of Volcán de Acatenango, above Las Calderas, alt. 2700–2900 m., Jan. 3, 1939, *Standley 61890* (FM). QUEZALTENANGO: pine-fir forest, Volcán Zunil, alt. 2500–3800 m., Jan. 22, 1940, *Steyermark 34720* (FM); Volcán Santa María, alt. 3260 m., July 27, 1934, *Skutch 869* (FM,TYPE, GH).

6. Smilacina macrophylla Mart. & Gal. in Bull. Acad. Brux. **9**[2]:387. 1842.

Stems 4.5–6.0 dm. high, somewhat flexuous, glabrous; leaves shortly petiolate or subsessile, ovate-lanceolate, acuminate, 12.5–22.0 cm. long, 2.5–9.0 cm. broad, with 5–10 prominent longitudinal veins and less conspicuous ones between, lateral veins visible in dried plants; inflorescence subspiciform, several-flowered, 12.5–22.0 cm. long, 1.2–2.0 cm. broad; peduncle straight, much stouter than the pedicels; pedicels solitary, paired or clustered, 3-5 mm. long, horizontal or descending; flowers white (?); perianth segments broadly oval, 6 mm. long, 3.0–3.5 mm. broad, nearly erect; stamens included, filaments enlarged at base, 3 mm. long, anthers 1.5 mm. long; ovary and style of equal length, 4 ovules to each loculus; mature fruit unknown.

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[19] **Smilacina scilloidea** Mart. & Gal. var. **rosea** Emons, var. nov., ab specie floribus roseis praecipue differt.

MEXICO: VERA CRUZ: barranco of Teoxolo, near Jalapa, alt. 3500 ft., May 22, 1899, *Pringle 7854* (GH, US); Huitamalco, June 1841, *Liebmann 14635* (US, FM).

I have not seen the type specimen of *S. macrophylla, Galeotti 5473,* but the plants cited above agree well with the original description.

7. Smilacina stellata (L.) Desf. in Ann. Mus. Par. **9**:52. 1807.

Convallaria stellata L. Sp. Pl. 316. 1753.
Tovaria stellata (L.) Neck. Elem. **3**:190. 1790, name only.
Maianthemum stellatum (L.) Link, Enum. **1**:343. 1821.
Asteranthemum vulgare Kunth, Enum. **5**:152. 1850.
Unifolium stellatum (L.) Greene in Bull. Torr. Bot. Club **15**:287. 1888.
Vagnera stellata (L.) Morong in Mem. Torr. Bot. Club **5**:114. 1894.

Stems 1.5–5.5 dm. high, somewhat flexuous, glabrous; leaves sessile, amplexicaul, narrowly eliptical-lanceolate, acuminate, 4–15 cm. long, 1.0–4.5 cm. broad, upper leaf-surface glabrous, lower surface pubescent, many parallel longitudinal veins more or less of equal prominence, lateral veins usually hidden; inflorescence typically racemose, 2.5–7.0 cm. long, 1.5–2.0 cm. broad; peduncles unbranched, more or less straight; pedicels solitary, 2–10 mm. long, ascending; flowers white; perianth segments narrowly eliptical-oblong, 5–7 mm. long, 1.5–2.5 mm. broad, spreading; stamens included, 4 mm. long, filaments somewhat enlarged at base, 3 mm. long, anthers 1 mm. or less long; ovary usually longer than style, 2 ovules to each loculus; mature fruit 1–2-seeded.

MEXICO: CHIHUAHUA: collected near Colonia Garcia in the Sierra Madres, alt. 2290 m., June 16, 1899, *Townsend & Barber 35* (FM, GH, MBG, UC, US). NUEVO LEÓN: in shelter of thickets below timberline, alt. 11,700 ft., Cerro Potosí, July 9, 1938, *Schneider 1033* (FM).

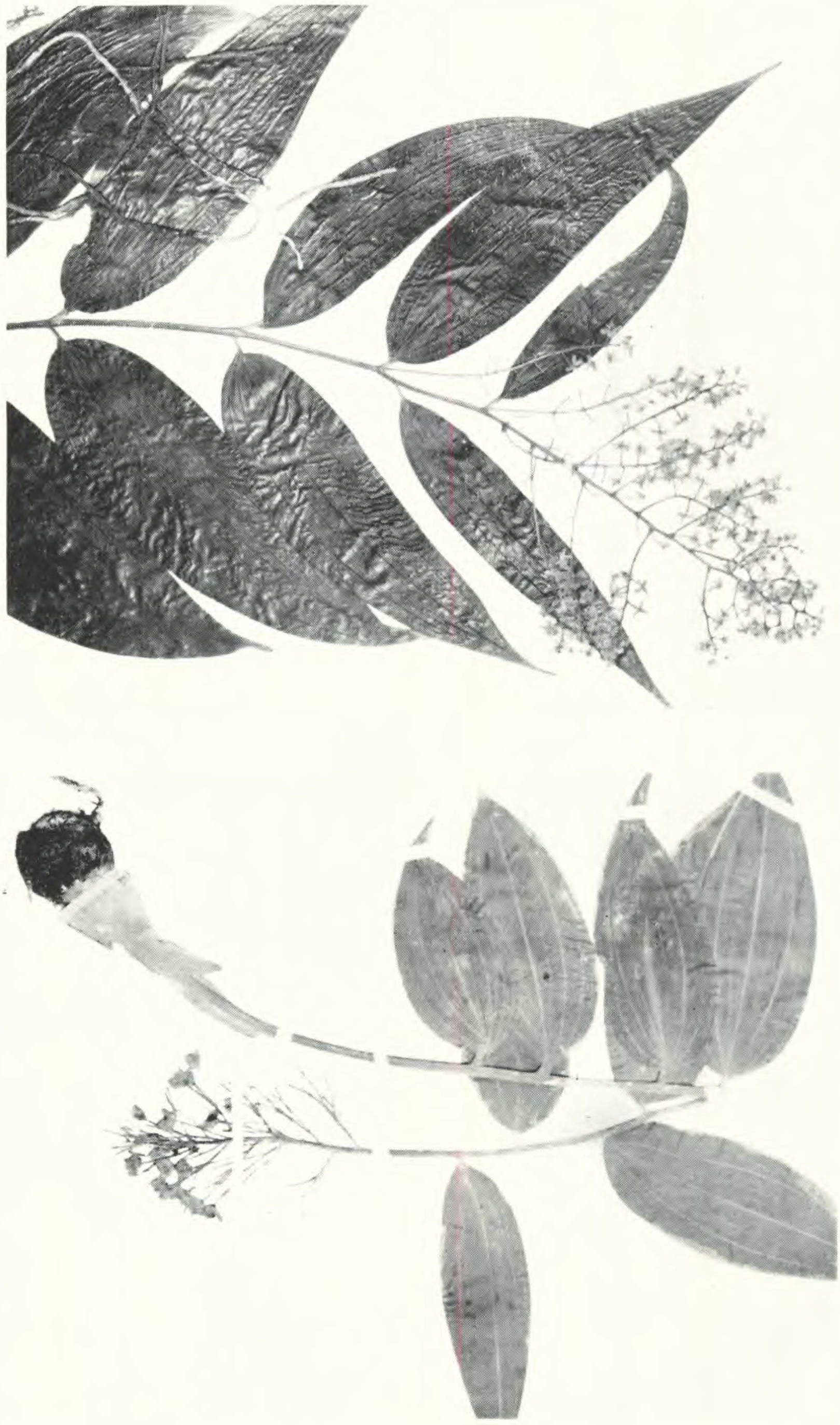
This species is chiefly one of the United States, and reaches only a limited portion of northern Mexico where it is found in the higher altitudes. It is easily distinguished by its pubescent, sessile leaves, and simple raceme.

Explanation of Plate

PLATE 18

Fig. 1. *Smilacina paniculata* Mart. & Gal. Specimen collected in Valley of the Upper Río Chiriquí Viejo, vicinity of Monte Lirio, Province of Chiriquí, Panama, *R. J. Seibert 184*, in the Herbarium of the Missouri Botanical Garden.

Fig. 2. *Smilacina amoena* Wendl. var. *Salvini* (Baker) Emons. Epiphyte collected along Quebrada Canjula, between Sabinal and Canjula, Volcán Tacana, alt. 2200–2500 m., Dept. San Marcos, Guatemala, *J. A. Steyermark 36024*, in the Herbarium of the Chicago (Field) Museum of Natural History.



EMONS—CENTRAL AMERICAN SMILACINAS

1

2

Explanation of Plate

PLATE 19

Fig. 1. *Smilacina flexuosa* Bertol. Specimen collected in Chicharras, Chiapas, Mexico, *E. W. Nelson 3762*, in the United States National Herbarium.

Fig. 2. *Smilacina macrophylla* Mart. & Gal. Specimen collected in barrancos of Teoxolo, Vera Cruz, Mexico, *C. G. Pringle 7854*, in the United States National Herbarium.

EMONS—CENTRAL AMERICAN SMILACINAS